ADDITIONAL NOTES ON THE GENUS AVICENNIA. V

Harold N. Moldenke

Herbarium acronyms employed in this and in all of the other installments of these "Additional notes" are explained in full in my "Fifth Summary", pp. 795—801 (1971) and its supplements.

AVICENNIA L.

Additional & emended synonymy: Horau Adans., Fam. Pl. 2: 80 & 585. 1763. Auicennia Reichard in L., Gen. Pl., ed. 8, index. 1778. Racua J. F. Gmel. in L., Syst. Nat., ed. 13, imp. 1, 2: 1612. 1789. Corna Noronha, Verh. Batav. Gen. 5, ed. 1, art. 4: 2. 1790. Racka Bruce ex J. F. Gmel. in L., Syst. Veg., ed. 13 rev., imp. 1, 2: 245, in syn. 1791; Wittstein, Etymol.-bot. Handwörterb. 749. 1852. Halodendron Roem. & Schult. in L., Syst. Veg., ed. 16, 3: 485. 1818 [not Halodendron P.DC., 1825]. Avicenia Dum., An. 22. 1829; Pfeiffer, Nom. Bot. 1 (2): 1847, in syn. 1874. Avicenia W. Griff., Notul. Pl. Asiat. 4: 173, sphalm. 1854. Avicinnia W. Griff., Notul. Pl. Asiat. 4: 189, sphalm. 1854; Ambasht, Text-Book Pl. Ecol. 169 & 191, sphalm. 1969. Avicenia L. apud Masamune, Sci. Rep. Kanazawa Univ. 4: 50. 1955. Avucemuia L. ex Moldenke, Phytologia 7: 140, in syn. 1960. Saltzmanna Roxb. ex Moldenke, Phytologia 7: 140, in syn. 1960. Avicenna Farnsworth & al., Lynn Index 6: 263, sphalm. (1969) and 7: 228. 1971. Avincennia Whipple, Journ. Elisha Mitch. Sci. Soc. 88: 13, sphalm. 1972.

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Type species: Avicennia officinalis L.

Horau Adans. is placed in the synonymy of Laguncularia Gaertn., of the Combretaceae, by Jackson (1893, 1946, 1960) and the only binomial published in it is a transfer from Laguncularia, but Airy Shaw (1966) and Dandy (1967) affirm that it actually belongs in the synonymy of Avicennia.

Padmanabhan (1962) comments that "Avicennia has been separated from the Verbenaceae on the basis of wood anatomy, articulate branches, imbricate scale-like prophylla, the free central placentation, and the pendent orthotropous ovules", but "The author has re-examined the question, and has come to the conclusion that 'the morphological modifications and degree of aggressiveness in the haustorial activity of Avicennia appear to be more of a quantitative variability than of a qualitative one.....a summation of embryological characters does not warrant the creation of an independent monotypic family to accomodate the genus Avicennia'".

On the other hand, however, it should be pointed out again that the Avicenniaceae, as a separate family, has been accepted

by many distinguished botanists in the past, including taxonomists, plant morphologists, wood anatomists, and ecologists, and is being accepted today by an ever-increasing number of careful workers. Among these may be mentioned Saint-Hilaire (1826), Endlicher (1838, 1841), Miquel (1845), Schnitzlein (1856), Bocquillon (1862), Eichler (1875), Van Tieghem (1898), Warming (1912), Small (1913, 1933), Van Tieghem & Constantin (1918), Record & Mell (1924), Record (1934), Frey-Wyseling (1935), Pulle (1937), Croizat (1944), Buswell (1945), Erdtman (1945, 1952, 1961), Alain (1946), Hodge & Gutierrez Villegas (1948), Barkley (1948, 1949), Den Berger (1949), Angely (1960, 1970), Allan (1961), Hepper (1963), Gooding, Loveless, & Porter (1965), Airy Shaw (1966, 1973), Duke (1969), D. S. & H. B. Correll (1972), Aubréville & Leroy (1972), Letouzey (1972), Jafri (1973), Mukherjee & Chanda (1973), Sowunmi (1973), Villiers (1973), Rouleau (1974), Täckholm (1974), Troncoso (1974), etc. Dandy (1967) says "Avicenniaceae, olim Verbenaceae". Airy Shaw, in the 7th and 8th editions (1966, 1973) of Willis' "A Dictionary of Flowering Plants", not only adopts it as a valid family, but relates it to the Salvadoraceae rather than to the Verbenaceae. Van Tieghem & Constantin (1918) actually create an order, Avicenniales, for it, including in the order also the Symphoremaceae and Harmandiaceae, and this classification is followed by Gibbs (1974), who notes that if the Avicenniaceae really belong in an order of the Santalineae, as Van Tieghem & Constantin maintained when they created the Order Avicenniales, then "we might expect its members to have acetylenic compounds, but I have no information on this point."

Barkley (1965) rightfully keeps Avicenniaceae as a separate family. He classifies it, along with the Symphoremaceae, Globulariaceae, Myoporaceae, Tetrachondraceae, Selaginaceae, and Lamiaceae, in the Order Lamiales (Order 83), but places the Verbenaceae, along with the Phrymaceae, Cordiaceae, Ehretiaceae, Chloanthaceae, Stilbaceae, and Duckeodendraceae, in a separate Order Verbenales (Order 61). He lists Hilairanthus as a valid genus, but in my opinion its characters are not sufficient to warrant its segregation from Avicennia.

Bharucha (1947) tells us that although Avicennia differs ecologically from land plants, it does not seem to differ physiologically from them during the first 8 days of germination.

Dieffenbach (1843) places the genus Avicennia in the Myoporineae (=Myoporaceae); Goyena (1911) regarded it as comprising the Tribe Avicenieas Meisn. Duke (1969) enumerates the following contrasting characters between the Avicenniaceae and the Verbenaceae: In the Avicenniaceae: germination phanerocatylar, one cotyledon conduplicate about the other, slightly unequal, broadly reniform, subcordate, sometimes emarginate; eophylls supracotyledonary, opposite, decussate with the cotyledons, entire, lanceolate to ovate, weakly penninerved. In the Verbenaceae: germination phanerocotylar, the cotyledons ovate, entire, subtriplinerved,

short-petioled; eophylls supracotyledonary, opposite, decussate with the cotyledons, more often dentate than the metaphylls; indument often diagnostic, e.g., the punctate glands of Tectona impart a red-spotted outline of the seedling to the newspaper in which it is pressed.

Mukherjee & Chanda (1973) have reviewed the "biosynthesis of Avicennia L. in relation to taxonomy" and conclude that "The common mangrove genus Avicennia is provided with some typical characters like differential wood anatomy, articulate branching, free-central placentation, 3-colporate pollen with lolongate ora and reticulate surface pattern, etc. These characters suggest that it should not be retained in Verbenaceae. The collective morphological (gross and pollen), and anatomical characters found in combination in Avicennia are not encountered in any other mangrove species. Avicennia happens to be the only verbenaceous member which serves as a major constituent of mangrove community. Gross and pollen morphological characters, typically found in Avicennia are not exhibited in any other member of Verbenaceae. It's affinity with Verbenaceae was drawn from the assumption that Avicennia originated from tropical East Asian and Malaysian Symphoremoideae consisting of Congea, Symphorema and Sphenodesme [now constituting the Symphoremaceae] during Tertiary Period and later flourished in the tropical coastal regions. Considering the above factors it seems that the segregation of Avicennia to form a family for itself is justified."

These authors state that "The characteristics of wood anatomy of Avicennia is [sic] different from the arboreal verbenaceous members. Although ecologically Avicennia is regarded as an important constituent of mangrove community, it has practically no anatomical resemblance with any other mangrove species....The characteristic vessels, fibres, ray and wood parenchyma, etc., of Avicennia present a distinct variability in wood anatomical structures from the scanty arboreal Verbenaceae. Moreover, the general outline of Avicennia stem is ribbed hexagonal while other verbenaceous members have either square or round or triangular ribbed stem. This may also be regarded as a criterion for segregation. Pollen morphologically Avicennia is distinctly different from all other verbenaceous members. The presence of tricolporate aperture with lalongate ora which are confined within the limits of colpi coupled with reticulate surface ornamentation are absent from other members (170 species from 55 genera) of Verbenaceae.....Pollen morphologically Avicennia pollen types are regarded as more advanced than any other verbenaceous member so far as primary and secondary characters, i.e., apertural configurations and surface patterns are concerned, as 3-colporate composite aperture with lolongate ora is considered to be more advanced than 3-colpate or 3-colporate with lalongate ora..... Regarding surface pattern, it is considered that these types which serve to provide maximum protection to germplasm are prim-

itive. Thus, the line of evolution is considered to run from grains with excrescences to grains without excrescences or tectum."

Bullock (1958) accredits the name, Avicenniaceae, to Schnitzl., Ic. Fam. Nat. 2: pl. 107 (1856), which is correct, but in his later (1959) work he credits it to Endl., Ench. Bot. 314 (1841). Endlisher, however, in the reference cited, proposed an "Avicennieae", not an Avicenniaceae. Saint-Hilaire (1826) similarly recognized the family status of the group, but did not propose the actual name which we must use for it now. It was Schnitzlein who actually first proposed the name with the proper family termination as now accepted. It is, therefore, Schnitzlein's name which should appear as authority for the name, not either Saint-Hilaire's nor Endlicher's.

Plant anatomists tell me that the anatomical wood characters of Avicennia are quite unique; embryologists and morphologists stress the very different ovary characters; ecologists stress the habit and habitat. Palynologists have recently done considerable work on the pollen of the genus. For instance, Mukherjee (1974) says "It may be postulated that the 3-colporate aperture with lalongate ora encountered in verbenaceous Avicennia.....in the course of evolution perhaps broke into two lalongate ora which got separated and gave rise to such apertural condition[s] as are found in the grains of Myoporaceae. This may give rise to apertural types encountered in Phrymaceae or perhaps the Avicennia pollen gave rise to the vestigeal type of di-orate condition encountered in Phrymaceae which ultimately culminated in Myoporaceae. This theory is strengthened by occasional presence of lalongate ora in Phryma. Punt (1967).....is of the opinion that palynologically the trend of evolution in composite apertural type runs from lalongate to lolongate ora to di-orate condition. Moreover, surface of pollen grains of Avicennia, Phryma and Myoporum, Eremophila and such other genera possess the same type of pattern. The morphological similarity between Myoporaceae and Avicennia as was suggested by Wernham (1912) is also in favour of the theory based on pollen morphology."

Croizat (1944) was of the opinion that Avicennia is "absolutely!" not a member of the Verbenaceae, but is "a strange child of the Dipterocarpaceae and the Ancistrocladaceae".

Chapman (1970) proposes the following ecologic group terms: Alliance Avicennietalia; Order Avicennion occidentalis (Associations Avicennietum nitidae and Avicennietum africanae) and Order Avicennion orientalis (Associations Avicennietum marinae, Avicennietum resiniferae, Avicennietum albae, Avicennietum officinale, Avicennieto albae-A. marinae, and Avicennieto-Excoecarietum).

Fryns-Claessens & Cottham (1973) report that Avicennia plants have diamesoperigenous type stomata in their leaves. Backer & Bakhuizen (1965) report that in Java Avicennia trees are sometimes deliberately planted between and along coastal fishponds.

Göbel (1905) affirms that "Avicennia forms, as it were, the transition amongst mangroves to the viviparous plants in which the fruit-wall is not bored through on the mother-plant; its seedlings are set loose, sometimes invested by the fruit-wall, at other times without it. They have stiff upwardly curved hairs upon their hypocotyl, and these serve for the first fixation in the mud." Ven Katesan (1966) describes the "seeds of Avicennia" as "semi-viviparous". He reports that in India the local species are occasionally used as rough walling, fuel, and a good fodder and that they are "non-copping". Navalkar (1956) reports that in the same country the growing leaves are fed upon by "cows, bulls, and buffalo". Thanikaimoni, in a personal communication to me, asserts that in parts of the Indian coast the leaves are so completely cropped that identification of the plants is often rendered very difficult.

Photographs illustrating the browsing of Avicennia plants by goats at Mizny, Gujarat, India. Photographs by courtesy of Dr. G. Thanikaimoni, Institut Français, Pondichery, July 23, 1975

Other authors have described the seeds as without endosperm and viviparous, with epigeal germination. Hepper (1963) speaks of the embryo as viviparous. Baker (1900) refers to "the plumule growing out before the seed falls". Ten & Keng (1969) maintain that "Avicennia seeds are viviparous, exhibiting epigeal germination. The well-developed embryo possesses a pair of leathery, conduplicate cotyledons. Leaves show typical xerophytic features. Stomata are Often of the caryophyllaceous type, and confined to the lower surface. Petioles are characterized on the adaxial surfaces by grooves which are lined by glands and trichomes. Three bundles form the vascular supply of the petioles. Young stems exhibit anomalous growth in the form of included phloem arranged in concentric rings. Phellogen arises subepidermally. In the vasculature of the 4-lobed corolla, 3 species have 4 traces each supplying cone corolla-lobe: in A. officinale [sic], an additional trace runs into the posterior corolla-lobe, This suggests that the 4-lobed corolla is probably derived from a 5-lobed form. The ovary is bilocular at the basal part, but in the upper level only a 4-angled central axis is present. The incompletely free-central placentation is probably a modification of the axile placentation."

Martin (1946) confirms the absence of endosperm. Rendle (1967) speaks of the stem increasing "in thickness by repeated production of new cambiums and concentric with the original one" and comments on the "unusual embryology" described by Treub (1883).

Letouzey (1972) says for A. africana that "cette graine germe sur l'arbre même, comme chez les vrais palétuviers." Villiers (1973) reports for what he calls A. germinans: "A. germinans est une plante vivipare: l'embryon se développe dans le fruit; il est déjà unde plantule quand il se sépare de l'arbre."

Yet in spite of all the above testimony, Uphof (1941) makes the amazing statement that there is no vivipary in Avicennia!

Williams (1949) avers that in Zanzibar members of this genus are known as "mchw" and that the trunks are used for fuel in lime-burning operations in less inundated sites.

Burkill (1966) gives the following brief review of the taxonomy and economic value of the genus: "The species of the Indian and Pacific Oceans have yellow flowers, while those of the Atlantic have white ones; there are other differences in the ovary and the embryo which marke them off into two botanical groups, but in general appearance they are very similar. The Asiatic species run into one another, and the views which have been published on their definition are most difficult to bring into line. The last, and probably the best on the Malayan species, is that to be found in Watson's account of the Mangrove forests (.....1928). He recognized four species: Ridley had recognized five, his fifth, A. sphaerocarpa, being represented by a Penang plant which Watson considers not to differ from A. intermedia. Bakhuizen (....1921), on the other hand, collected all the Malayan plants known to him into two species, and Merrill (.....1923) followed him. The simpler division of Bakhuizen and Merrill admits A. marina as a

tree with small flowers only half a centimeter across (2/10 in.), and holds A. officinalis to be a tree with large flowers, 1 — 1 1/2 cm. across (4/10 — 6/10 in.); Bakhuizen supplements this by differences in the amount of silky hair on the ovary and in the stigma. Ridley's and Watson's A. officinalis is the same species as Bakhuizen's and Merrill's; their other species are put into Bakhuizen's A. marina, but, of this, varieties are freely recognized.

"Against Bakhuizen's classification one obvious objection is found in the dissimilarity of the habitat of the Red Sea plant, which is the original A. marina, on the shore of a very saline sea, and his A. marina var. alba, which is found away from the salt water, up creeks into which an abundance of fresh water descends. This plant will here be called A. alba, as it seems best to regard it as a species. Watson gives its flowers as the least of the four in Malaya, but the flowers of A. intermedia and A. lanata are only a trifle larger. The fruit of A. officinalis is the largest and thickest through; the others constitute a series from A. marina to it.

"It is useless to endeavour to assign much of what has been written on the utility of Avicennias to particular species, and it will not be attempted here.

"The Malays and Javanese call all the species 'api-api', and as showing that this name is an old one, it may be added that it is used in the form of 'afi-afi' in Madagascar. The Siamese call all 'sama tale'. Apparently the Semang use 'itil' for any of them, and 'ki balanak' is a comprehensive Sundanese name.

"The timber (Foxworthy.....1921) is hard and moderately heavy; very coarse-grained; brittle, but difficult to split; the sap-wood pale grey; the heart-wood, when present, olive-brown to purple; and it is interesting that when freshly cut the heart-wood floats, but the sap-wood sinks. As the trees are usually crooked, no length of timber can be got. It gives indifferent firewood. Writers such as Low and McNair did not refer to it when calling 'api-api' a very good or excellent firewood, for indeed it is not liked because it cannot be split, though the name 'api-api' may indicate firewood. It is used, however, when better is not easily procurable. It burns smoulderingly. The fisher-folk like it for smoking fish, to which it is said to give an agreeable flavour. It is used, also, for smoking rubber.

"Foxworthy summed up regarding it: 'altogether it is a very unsatisfactory wood — the least useful of the mangrove-swamp woods -- and the tree is usually considered as a weed in the swamp.

"The durability is said to be poor, though beetles rarely attack it. Foxworthy & Woolley (....1930) showed this by experiments. It is used for rice-mortars and has been suggested for paving-blocks (Schneider.....1918); but the last seems unreasonable.

"Its structure is peculiar, by reason of an irregular layering, which one writer has tried to connect unsuccessfully with the periodicity of spring and neap tides (see Gamble....1922....and Baker...1916). Baker, commenting on the structure, compares it to 3-ply wood on account of the crossing of the grain, and he adds that though it will not split radially it is more easy to split tangentially than any timber known to him. The Australian aborigines, taking advantage of this, made shields from it. Baker declares that it is impossible to kill the tree by ringing it, as a result of the structure of the stem.

"This structure has been described in considerable detail by him (op. cit.) and by Jansonnius (....1926...). Older writers have said that the bark serves as a tanning agent in India and elsewhere; but in reality it is of little use in tanning. Pilgrim (.. 1924...) says of the genus in Tenasserim: 'the bark will make leather, but its analysis always gives poor figures for tannin-content (2.5 to 5 per cent)....Baker....similarly gives the tannin-content as low. Nevertheless, Gerini (...1911...) says that nets are dyed brown with its bark; to which statement it may be added that further investigation is indicated.

"The fruit may be eaten at times, Bakhuizen quotes an Arab author, who says that it causes dizziness. Rumpf recorded it as a famine-food of Celebes — not the whole fruit, but the seeds, which are boiled and soaked in water for a fortnight to remove their acridity as far as possible, before they are eaten. K. Heyne (....1927..), after repeating this, adds that the fruit may be eaten even in normal times by the fisher-folk of Celebes, and in Java. About Batavia, the fruit is boiled and then sun-dried.... Ridley records, against a specimen of A. officinalis, that it may be eaten in Singapore. Watt...., without giving precise information about localities, says that the kernels are bitter but edible: presumably he meant that they are eaten in India. Baker.....says that the aborigines of Australia freely eat the fruits roasted.

"About the Red Sea and the Persian Gulf, where fodder is a thing of much value, the leaves of A. marina are eaten by camels..... Paranjpye (....1920...) says that branches of Avicennia are cut and fed to cattle in the Ratnagiri district of the west coast of India. He calls the species A. officinalis, probably meaning either of the two which may occur there. It is not known that Avicennia leaves are used elsewhere, but it is interesting to know that they can be used.....Baker....says that cattle eat the leaves of the Australian Avicennia, or Grey Mangrove, with great relish.

"A green, bitter and somewhat aromatic resin oozes from the bark. This resin is medicinal round about the Indian Ocean. An Arab writer calls it an aphrodisiac, and adds that it may also be applied for toothache. In western Java it is considered a contraceptive, and is taken over indefinitely long periods....This use is given also by Ridley as known among the Malays...but in his prescription the abortient juice of a young pineapple is associated. Watt....says that the roots possess aphrodisiac properties. He says that unripe seeds are used as a poultice to hasten boils

and abscesses to maturity. His information is given under the name A. tomentosa, but may apply to any one of the Indian species.

"The ash, after burning the wood, is used as soap in India.... and Baker tells us that early settlers used it similarly in Australia. There is a large amount of alkali in it. Baker gives an analysis. Wood-tar was made from it experimentally by Wells, and reported on (1917)."

Brown (1969) reports that "the respiratory gaseous exchanges of detached whole mangrove seedlings of the genera Avicennia, Bruguiera, and Rhizophora in a range of O_2 concentrations from 0.21 percent (air) were markedly reduced by the presence of external CO_2. Aerobic respiration decreased steadily for 16 days but the respiratory quotient (RQ) remained at unity. In anoxia CO_2 output fell to half that in air. Ethanol accumulation was negligible but, relatively, acetaldehyde values were higher than in older tissues. Lactate accumulated initially but later decreased. On return to air CO_2 output was elevated above control values in a pattern resembling the previous lactate accumulation. The extent of the burst was too great, and the RQ too low, to be explained entirely by lactate oxidation. In 5 or 10 percent O_2 the CO_2 outputs were below those in inoxia and the RQ eventually rose to 1.4 suggesting the induction of fermentation. The absence of ethanol, acetaldehyde or lactate indicates that CO_2 was released from reactions other than those in the Embden-Meyerhof pathway. Tissue slice CO_2 outputs decreased with lowered O_2 concentrations and the RQ was always above unity except in air. The burst on return to air was absent, suggesting that slicing affects decarboxylation mechanisms."

Stace (1966) checked the leaf epidermal characters of 8 mangrove genera in the Combretaceae, Rhizophoraceae, and Avicenniaceae with each other and with non-mangrove genera in the same or reputedly related families. He states that "mangrove genera share a number of common features, but are easily separated into 3 groups coinciding with the 3 families. Differentiation by epidermal characters thus clearly parallels that by characters more usually used in plant taxonomy."

Gibbs (1975) reports the presence of lapachol (a 1,4-naphthaquinone) and tannins, but the absence of leucoanthocyanins and the absence or probably absence of saponins.

Gessner (1967) states that Avicennia species store less water in their leaves than do Rhizophora species. Removal of all pneumatophores caused no visible harm to the plants even after many months. Pneumatophores similar to those in Avicennia are seen also in Sonneratia.

Breen & Hill (1969) investigated the events that led up to the mass mortality of mangroves in the Kosi estuary in 1965 and have concluded that flooding of the estuary following the closure of the mouth for 5 months was responsible. "Avicennia marina, will, however, probably make a comeback and remain there."

Macbride (1960) says for the genus Avicennia as a whole that

"The dark brown hard wood is very durable. The name recalls Ibn Sina, erudite Persian" physician of Bokhara, born in 980, died in 1037, whose "Quan um" (canon of medicine) was a synthesis of all the medical knowledge and wisdom available at the beginning of the 11th century in that part of the world.

Thomson (1964) avers that the leaves, flowers, and fruits of Avicennia are eaten by hoatzins (Opisthocomus hoatzin) in northern South America.

Van Steenis (1969) claims that the stratigraphic distribution of Avicennia pollen in northern South America and in Nigeria goes back to the Upper Miocene; Muller (1964) reports it in the Lower Miocene of Borneo, while Fosberg (1969) tells us that the Middle Miocene in Borneo has "Avicennia type" pollen well preserved in fossil form. In this connection it should be recalled that A. eocenica Berry is described from the Eocene of Tennessee, A. germinans (L.) L. from the Pleistocene of Trinidad, A. lanceolata (Engelh.) Moldenke from the Tertiary of Colombia, A. miocenica Berry from the Miocene of Colombia, and A. nitidaformis Berry from the Eocene of Mississippi.

Caratini, Blasco, & Thanikaimoni (1973) comment that "The mangroves are [form] tidal forests which occupy an exacting littoral habitat, almost invariably salt or brackish water and coastal silt: clay and sand in various proportions, in exceptional cases sand only. Their distribution is restricted to tropical shores.....The presence of pollen grains of Rhizophoraceae, Nypa and Sonneratia in a given sediment imply the occurrence of a mangrove [forest] in the immediate vicinity. Palynological studies (Muller, 1964) have revealed the presence of mangroves in the Quaternary and Tertiary periods. Such studies not only give us an idea of the palaeoclimate but sometimes even permit us to locate the ancient shore lines....Three principal vegetation zones can be recognized in the mangrove region of Pichavaram [India] viz. Rhizophora zone, Avicennia zone and back-mangrove [a bushy formation of mostly halophyte shrubs]. The pollen analysis of recents (sic) sediments from this region gives an image of the vegetation quite different from the actual floristic composition. The extent of this deviation seems chiefly due to the over-representation of the pollen grains of Rhizophoraceae and Sonneratiaceae, under-representation of the pollen grains of Avicennia, absence of the pollen grains of several mangrove species and the presence of a number of allochthonous pollens which constitute nearly 25 percent of the total pollen grains extracted from the sediments."

Cooke (1961) records the fungus, Schizophyllum commune, from Avicennia stems; other workers have found members of the genus attacked by Leptosphaeria avicenniae, Mycosphaerella pneumatophorae, and Sphaeronema avicenniae. Rogerson (1971) adds Macrophoma sp., Rhabdospora avicenniae, and Zalerion varium to the list, while Kohlmeyer (1968) lists Didymosphaeria enalia, Lul-

worthia sp., Parliomyces lentiferus, Torpedospora radiata, Culcitalna achraspora, and Phoma sp.

Rehm & Humm (1973) report that Sphaeroma terebrans, wood-boring isopod, is destroying the prop roots of red mangroves (Rhizophora mangle) along the southwestern coast of Florida to such an extent that the Ten Thousand Islands and mangrove fringes of the mainland are steadily shrinking. What effect this will have on the Avicennia communities of the region is not yet obvious. Mangroves of the Florida Keys (on the east coast) are as yet free of this wood borer.

It is probably worth recording here that the original notation by Linnaeus relating to Avicennia (1735) reads "Avicennia † Oepa HM." Planer (1775) lists the German vernacular name, "Avicennie". One of the earliest references to Avicennia is that of P. Hermann (1726) who records it as "BULATWAELA Tambul pro Tembul Avicennae. Betre. Garc. Betele Vid. fol. 32."

The Endlicher reference cited in the bibliography of this genus is often cited as "1836-1856", but the pages involved here were actually issued in 1838. The Foreman (1972) reference has "1971" on its title-page, but was not actually issued until 1972. The Angely (1971) reference is often cited as "1970", but was not actually published until 1971; the Emould (1922) reference has "1921" on its title-page. The Schumann & Lauterbach (1900) reference bears a "1901" date on its title-page, but was received in the New York Botanical Garden library on July 12, 1900.

The Palisot de Beauvois, Fl. Oware reference is often cited as "1805" or "1809", but actually was published in 1806; similarly, the W. Griffith (1846) reference is often cited as "1851", the title-page date, but pages 1--162 actually appeared in 1846, pages 163--358 in 1847, and only pages 359--510 in 1851.

Villiers (1973) asserts that "Avicenia" is used by Linnaeus in his Sp. Pl. 1: 110 (1753) and "Avicenna" on page 116 of the same work, but I fail to find either word used on the pages specified.

Clarke & Hannon (1970) report that the tolerance of Avicennia and Aegiceras seeds and seedlings to seawater in the Sydney, Australia, region is greater than that of Triglochin, Sporobolus, and Juncus, but less than that of Arthocnemum and Suaeda of common mangrove formation genera there. Huxley & Bramwell (1973) report that in southeastern Asian mangrove formations the carnivorous mudskipper, Periophthalmodon schlosseri, makes its home in the firmer mud within the fringe of the Avicennia zone.

Ogura (1940) asserts that, unlike those of Urandra, but like those of Sonneratia, the aerial roots of Avicennia are essentially dissimilar in structure (cortex and vascular bundles) to the subterranean ones. The thick aerial root of Taxodium is also similar but is formed by an abnormal growth of the dorsal part of the subterranean root. "These aerial roots of Sonneratia, Avicennia and Taxodium are believed to be developed for respiration and are called in general, since Goebel (1886), as respiratory roots, though

recently Troll and Dragendorff (1931) describe them as organs, which furnish the places for branch roots."

Puri (1960) reports that Avicennia is associated with Rhizophora and Acanthus on the west coast of Malabar and is a common shrub there. In the edaphic forests on Coco Island inward from the beach there is an edaphic mangrove swamp in the lower ground and on the ridges, including Avicennia, Rhizophora, Bruguiera, Ceriops, and Aegiceras. It occurs in the edaphic tidal forests in the Ganges delta and in the mouths of other rivers; also with Ceriops roxburghiana in the low edaphic mangrove forests along the edges of waterways in river deltas on the east coast of India, and a little on the west coast on soft tidal mud submerged by salt water at evertide, forming dense forests of low trees 10—20 feet tall. It is common also in the Sunderbans forests and the southern part of the Ganges delta where the mangrove formation has much fresh water carried in from the rivers and is composed most densely of Rhizophoraceae. The edaphic mangrove forests of Bombay Presidency include Avicennia officinalis. It grows with Rhizophora mucronata on the perpendicular banks of the Chakaria Sunderbans in India.

Berry (1972) has studied the fauna of the Malayan mangrove lagoons and has found there 8 species of polychaete worms, 1 sipunculate worm, 34 crustaceans, 11 bivalves, 35 gastropods, and 5 mudskippers.

Richards (1964) reports that in the regions of the world with tropical rainforests "marine angiosperms are less abundant. The Rhizophora community may persist for a long time as a nearly pure consocies or it may change rapidly by the invasion of other species which are able to grow on the firm soil and in the shelter provided by the Rhizophora. If the community changes, an inner zone of the mangrove Avicennia, generally associated with low-growing salt-marsh plants, may develop....In the 'Avicennia-salt-marsh associes'.....behind the outer Rhizophora consocies, on land which is regularly or only occasionally submerged, there is typically a zone dominated by Avicennia nitida. This forms an open forest, in striking contrast to the thickly tangled Rhizophora consocies, with an undergrowth of succulent shrubs, such as Batis maritima and Salicornia perennis and salt-marsh grasses. Where the ground level is low there may be little undergrowth, but typically the dense stand of salt-marsh plants among the pneumatophores of the Avicennia is characteristic. The 'Avicennia-salt-marsh associes' is best developed on land which is not regularly flooded by the tide. The Avicennia trees are not rapidly replaced by natural regeneration and as they die the forest becomes more and more open, with an increase in the salt-marsh vegetation or an invasion of species from the Conocarpus associes which often adjoins the inner edge of the Avicennia zone. If the trees disappear entirely an open salt-marsh or meadow may take the place of the mangrove swamp....The semi-mangrove, Conocarpus erectus,

though not always abundant, is the most characteristic species in [the 'Conocarpus transition associes]; it occupies a zone seldom reached by the tides, immediately behind from the Avicennia associes. Like the Avicennia zone, the Conocarpus associes is an open stand of tress and shrubs with an undergrowth of low-growing salt-marsh plants.....On parts of the Florida coast there is a very tall luxuriant mangrove forest [the 'mature mangrove forest association'] in which about 60 percent of the tall trees are Rhizophora and about 30 percent Avicennia.....The main line of...succession appears to be from the 'pioneer Rhizophora family' to the 'mature Rhizophora consocies' and from this through the 'Avicennia-salt-marsh associes' and the 'Conocarpus Transition Associes' to 'hammock forest', the climatic climax of the region....it will be evident that great changes in the environment take place during the course of the succession. Owing to the interaction of the vegetation and its habitat, the ground level rises. In the pioneer stage the vegetation is almost continually under water, but in the later stages the frequency of submergence diminishes till in the Avicennia and Conocarpus stages tidal flooding becomes quite infrequent. Accompanying these changes in the relative level of the land and water there are changes in salinity. The average salinity reaches a maximum in the Avicennia stage and afterwards decreases until it approximates to the value for inland soils. In none of the mangrove communities is salinity constant. It varies most in the Avicennia consocies where the ground and surface water is only occasionally renewed by the tide. Here the salinity may rise to very high levels in dry weather, while after heavy rain it may fall very low. Apart from the remarkable ability of the seedlings to establish themselves under tidal conditions, and the plant's tolerance of prolonged flooding at all stages of its development, the faculty of growing in media of high and often variable salinity is the chief physiological characteristic of mangroves. Yet since Rhizophora and even Avicennia grow naturally where the ground water is apparently perfectly fresh... it may be concluded that at least the American mangroves are salt-tolerant and not salt-demanding, that is to say they are facultative rather than obligate halophytes. This view is supported by a certain amount of experimental evidence. Von Faber (1923; also in Schimper, 1935) disagrees with this view, but the eastern (Old World) mangroves to which he refers are possibly different in this respect....In the Cameroons Rhizophora mangle forms the pioneer community on the seaward fringe and Avicennia grows further inland. Still further from the shore the mangrove passes into a brackish-water community dominated by a species of Pandanus in which palms (Raphia sp., Calamus sp., Phoenix reclinata) are common.....In Malaya the pioneers are not species of Rhizophora, but Avicennia alba and A. intermedia, or sometimes, on deep mud rich in organic matter, Sonneratia griffithii. These pioneer forests establish themselves on shoals or sandbanks out at sea which are exposed at neap tides, or along the seaward edge of existing for-

ests. Avicennia intermedia grows on a comparatively firm clayey substratum which is easy to walk on, A. alba and Sonneratia on softer and blacker mud. On the clay soils the Avicennia is normally succeeded by Bruguiera caryophylloides, but where Sonneratia is the pioneer, Rhizophora mucronata usually follows on..... The Bruguiera caryophylloides type [of mangrove forest]...occurs at a higher level than the preceding and forms a nearly continuous belt behind the Avicennia forest along the west coast of the Malay Peninsula, interrupted only by small stretches where Avicennia forest merges directly into Rhizophora forest. The soil is a firm stiff clay above the reach of the ordinary tides and flooded only during the day or two before and after the spring tides. This type is found chiefly on the sea-face and is usually absent both on shoals and in river forests."

Chapman (1970) discusses the phytogeography of mangroves and points out that the American Rhizophora mangle occurs in the Fijian, Tongan, and New Caledonian islands but not the American species of Avicennia and nowhere between these islands and the Americas. "Unless ocean currents across the Pacific carried the viviparous Rhizophora seedlings from Central America to Fiji they could only have arrived there by the agency of primitive man conveying them. This is not inconceivable since Heyerdahl has argued that voyages did take place between America and Polynesia. In such event, however, one would have expected some of the intervening islands to have received seedlings. It is difficult to accept the viewpoint that originally they occurred there and have since disappeared. The second feature of interest is the absence of the other New World mangrove with viviparous seedlings (Avicennia nitida) from Fiji and Tonga and the intervening islands. If ocean currents were responsible for Rhizophora mangle in these islands there seems no reason why Avicennia nitida should not be there also. This could form an argument in favour of human transport, but this then raises the question why Rhizophora seedlings should have been conveyed and not Avicennia seedlings. The answer could be found in the uses of the two plants by the primitive peoples of Central America. It is possible that the early natives did recognize the value of Rhizophora bark for the purpose of tanning rope, fishing nets and sails and took the seedlings with them on that account. Avicennia has no such useful function and therefore would be left behind. Transport also must have taken place very early before New World speciation had occurred because [the Pacific coast] Rhizophora harrisonii has not yet been recorded from Oceania."

The R. M. King 1550 and A. Gentry s.n. [August 4, 1967], distributed as Avicennia, are actually Laguncularia racemosa Gaertn. f. The genus Aganon Raf., often classified here as a synonym, is apparently neither avicenniaceous nor verbenaceous. Balakrishnan NBK.382, Bembower 72, and Tyson 5384 are also neither avicenniaceous nor verbenaceous. Bontia daphnoides L. is sometimes

distributed in some herbaria as an Avicennia, but it belongs in the Myoporaceae.

Excluded species are:

Avicennia agallocha Puri, Indian Forest Ecol. 232, sphalm. 1960 = Excoecaria agallocha L., Euphorbiaceae

Avicennia latifolia Hornem. ex Moldenke, Phytologia 7: 144, in syn. 1960 = something in the Myrtaceae

Avicennia mucronata Cloudsley & Thompson, Terrest. Environ. 36, sphalm. 1975 = Rhizophora mucronata Lam., Rhizophoraceae

AVICENNIA AFRICANA P. Beauv., Fl. Oware 1: 79—80, pl. 47. 1806.

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[to be continued]